Reference: *Biol. Bull.* **191:** 367–373. (December, 1996)

Chemical Induction of Larval Settlement Behavior in Flow

MARIO N. TAMBURRI[1,*], CHRISTOPHER M. FINELLI[1],
DAVID S. WETHEY[1], AND RICHARD K. ZIMMER-FAUST[2]

[1]*Department of Biological Sciences, Marine Science Program, and Belle W. Baruch Institute for Marine Biology and Coastal Research, University of South Carolina, Columbia, South Carolina 29208; and* [2]*Department of Biology, University of California, Box 951606, Los Angeles, California 90095-1606*

Abstract. The ability of dissolved chemical cues to induce larval settlement from the water column has long been debated. Through computer-assisted video motion analysis, we quantified the movements of individual oyster (*Crassostrea virginica*) larvae in a small racetrack flume at free-stream flow speeds of 2.8, 6.2, and 10.4 cm/s. In response to waterborne chemical cues, but not to seawater (control), oyster larvae moved downward in the water column and swam in slow curved paths before attaching to the flume bottom. Effective stimuli were adult-oyster-conditioned seawater (OCW) and a synthetic peptide analog (glycyl-glycyl-L-arginine) for the natural cue. The chemically mediated behavioral responses of oyster larvae in flow were essentially identical to those responses previously reported in still water. Our experimental results therefore demonstrate the capacity of waterborne cues to evoke settlement behavior in oyster pediveligers under varying hydrodynamic conditions.

Introduction

Larval recruitment is a major factor regulating the population dynamics of marine benthic invertebrates (Gaines *et al.*, 1985; Roughgarden *et al.*, 1988; Underwood and Fairweather, 1989; Menge, 1991). Two fundamental steps in the recruitment process are settlement and metamorphosis. The transport and delivery of planktonic larvae from the water column to the seabed is the settlement stage (Butman, 1987; Eckman, 1990; Gross *et al.*, 1992). Once a substrate is accepted, larvae then metamorphose into the juvenile form (Morse *et al.*, 1979; Burke, 1983; Crisp, 1984; Bonar *et al.*, 1990).

Neither sessile nor sedentary invertebrates travel far, if at all, after metamorphosis. The ability of their larvae to select appropriate substrates is therefore critical to adult fitness (Grosberg, 1987; Levitan, 1991). Commonly, substrate discrimination is based on chemical cues associated with predators, competitors, conspecifics, or food (Burke, 1984; Woodin, 1987; Johnson and Strathmann, 1989; Morse and Morse, 1991). These cues are thought to be mostly non-waterborne and detected after larvae contact surfaces (see reviews by Morse, 1990; Pawlik, 1992).

Settlement induction by waterborne substances is often considered to be unlikely for weakly swimming invertebrate larvae (Crisp and Meadows, 1962; Butman, 1989). The locomotory speeds of these larval forms are typically lower than horizontal water-flow velocities in benthic boundary layers, even at distances of less than one larval body length above the seabed (Butman, 1986). Yet behavioral responses to chemical cues in the water column might effectively enhance larval settlement onto the substratum under some circumstances. A recent model suggests that by responding quickly to a waterborne cue, weakly swimming larvae might change their vertical distributions in the water column (making more larvae available to be swept near the substratum by fluid flow) and thus dramatically alter their patterns of settlement (Eckman *et al.*, 1994).

Oyster larvae provide a valuable tool for assessing the role of waterborne chemical cues as agents mediating settlement in flow. In assays conducted in still water, oyster

Received 16 May 1996; accepted 23 September 1996.

* Current address: Monterey Bay Aquarium Research Institute, P.O. Box 628, Moss Landing, California 95039.

(*Crassostrea virginica*) pediveligers respond to dissolved chemical cues by moving downward in the water column and attaching to the bottoms of test chambers (Tamburri *et al.*, 1992; Zimmer-Faust *et al.*, in press). The stimuli are small basic peptides (*ca.* 500–1,000 Da) released into seawater by adult conspecifics (Zimmer-Faust and Tamburri, 1994). A potent analog for the natural cue or cues is the tri-peptide glycyl-glycyl-L-arginine (GGR), maximally effective at 10^{-8} *M*.

These waterborne chemical cues may also influence oyster settlement in flowing water. In flume assays, significantly more oyster larvae accumulate on substrates in target wells releasing the synthetic peptide analog than on substrates in seawater alone (Turner *et al.*, 1994). Such distributions could result because the larvae respond to chemical cues either in the water column or after contact with test substrates. To further establish the capacity for settlement behavior in flow, we quantify the movements of oyster larvae suspended in a small racetrack flume. Our results clearly demonstrate chemical induction of settlement from the water column under hydrodynamic conditions approaching those in nature.

Materials and Methods

Larval cultures

Larvae of *Crassostrea virginica* were maintained on a 12:12 D:L cycle (light on: 0700 h) at 1.0/ml in a 1:1 mixture of oceanic and artificial seawater medium (25°C and 25‰ salinity). Cultures were actively aerated and gently stirred by air bubbled through Pasteur pipettes. Marine flagellates (*Isochrysis galbana* and *Pavlova lutheri*) were provided as food at 2.5×10^4 cells/ml once each day. All experiments were begun within 6 h after 95% of the larvae in culture had developed eyes, and experiments were run for 24 h thereafter (Tamburri *et al.*, 1992). These conditions were in effect for larvae aged 19–21 days post-fertilization.

Chemical solutions

Procedures for making solutions were similar to ones previously described (Tamburri *et al.*, 1992). Both oyster-conditioned seawater (OCW) and 10^{-8} *M* GGR were used as test stimuli, and natural seawater (alone) was employed as control. Because a large volume of freshly prepared OCW was required in each trial, tests with this solution were limited to a speed setting of 2.8 cm/s. In contrast, trials with GGR and seawater (control) were conducted at speed settings of 2.8, 6.2, and 10.4 cm/s. Each test or control solution was prepared and filtered to 1.0 μm within 1 h before use. All experiments were conducted with solutions held at identical temperature and salinity as larval cultures.

Flume design

To minimize the number of larvae and the volume of test solutions needed per trial, all experiments were conducted in a small (40-l capacity), plastic racetrack flume (Fig. 1). The flume was 20-cm wide, consisting of two semicircular ends (20-cm radius at inner walls) and two straight sections (120-cm long). With 40 l of water, depth measured 5 cm. In one straightaway section, water flow was generated through the use of a digitally controlled motor-driven paddle wheel (48-cm total diameter) with a minimum bottom clearance of 0.3 cm. The drive wheel consisted of 12 paddles (7 cm $\times$ 19.2 cm), each tilted so that it exited vertically from the water on upstrokes. To reduce across-stream fluid motion, polycarbonate sheeting was placed parallel to the curved flume walls in the first turn to act as flow straighteners. At the downstream end of the second straightaway section, a working area was designated in which velocity profiles were taken and movements by larvae were video-recorded.

Velocity profiles were determined at each of three speed settings (2.8, 6.2, and 10.4 cm/s free-stream flow velocity, respectively) using a hot-film anemometer (TSI 1053-B). At each speed setting, a conical platinum film sensor (<1 mm diam, TSI model 1231W, 10°C overheat) was used to measure velocity at 16 heights above the flume bottom. These data were collected at 1 Hz, using a data logger (Campbell, Model CR10). Mean flow speed at each setting and height was determined by averaging measurements over 1-min intervals. To establish the shear velocity (U_*) for flow at each speed setting, mean flow velocities were regressed against the natural logarithm of height above the flume bottom (Nowell *et al.*, 1981; Jonsson *et al.*, 1991).

Experimental protocol

Separate trials were performed in the flume with either OCW, GGR, or seawater (control) at a uniform concentration mixed throughout the water column. In each trial, we suspended 2000 ± 358 (range) larvae in a beaker with 200–300 ml of seawater. The larvae were then gently poured from the beaker (over 5–10 s) into the flume at a site raised about 4 cm above the bottom and 1.0 m upstream of the working section. Video-recording was limited to the first pass of larvae over the working section. The flume was drained and then cleaned with several rinses of distilled water between each trial. Six trials were run for each solution at the two slowest speed settings, and three trials each at the fastest speed.

Video imaging and motion analysis

Simultaneous video-recordings from two cameras (Panasonic WV-BL-600), each equipped with a 55-mm

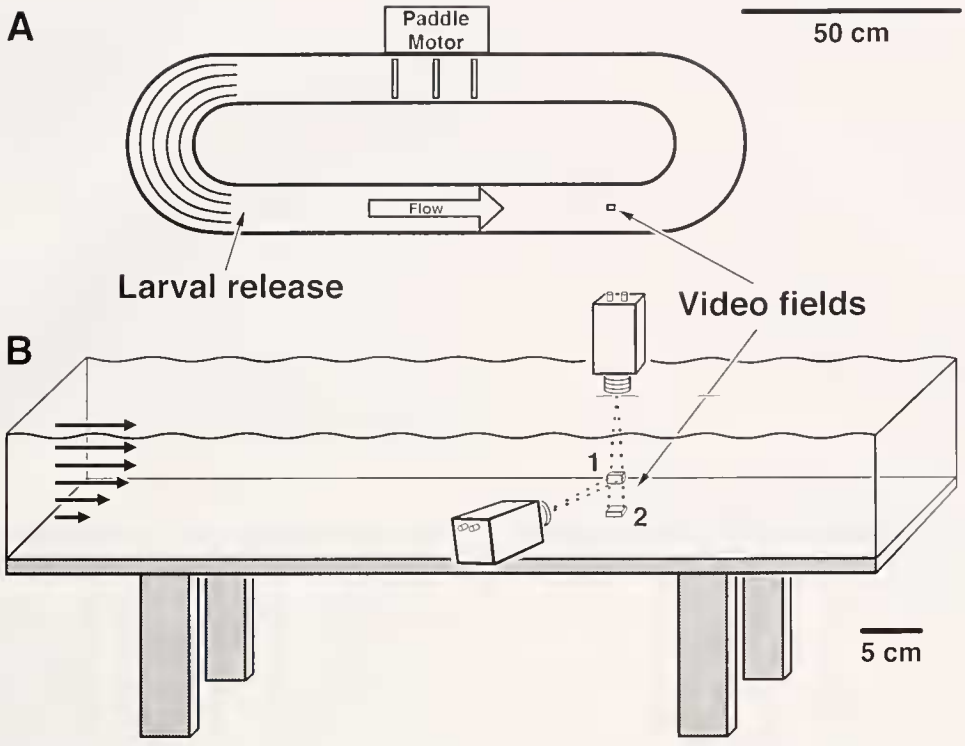

Figure 1. Schematics showing the small racetrack flume used in this study. In each trial, the flume was filled with 40 l of either oyster-conditioned seawater (OCW) or glycyl-glycyl-L-arginine (GGR) at a uniform concentration, or with seawater control. Following their release, larvae were video-recorded as they passed for the first time over the working area. (A) Top view indicating the direction of water flow, position of the paddlewheel, site at which larvae were released, and position and size of the working area in which video records were made. (B) A 3-dimensional view more closely indicating the video fields viewed by each of our two cameras. 1 = vertical field in the water column as viewed by the side-mounted camera. 2 = horizontal field in the bottom boundary layer as viewed by the overhead-mounted camera. Each field was 1.2-cm long and 0.7-cm wide, with a focal depth of 0.4 cm.

macro-lens, were made as larvae passed through the working section. One camera was mounted above and the other to the side of the flume (Fig. 1). Outputs from both cameras were run through a video splitter (American Dynamics, model AD1470A), recorded onto a single tape, and viewed on a monitor. The entire working section was illuminated with dim, far-red light (>650 nm). The side-mounted camera was positioned to view larvae in the free-stream, a minimum of 1.9 cm above the flume bottom. In contrast, the overhead camera was placed to view larvae within the boundary layer at heights between 0 and 4 mm above the bottom. By using a 4-mm focal depth in video-recordings, individual larvae could be tracked over the entire length of each video field. The field size recorded by each camera was 1.2×0.7 cm with the long axis parallel to the direction of water flow. Estimates of settlement activity were, therefore, made only for those larvae in the video field.

Methods for quantifying larval movements were identical to those previously described (Tamburri *et al.*, 1992; Tamburri and Zimmer-Faust, 1996). Video records were processed at 30 frames/s through a motion analyzer (Motion Analysis Corp. model VP 110 and ExpertVision software) interfaced with a Sun Microsystems SPARC IPC computer workstation. Because of the small video field (1.2×0.7 cm), both vertical orientation and speed at which larvae moved either upward or downward in the water column could be accurately determined only in the slowest flow (2.8 cm/s). Vertical motion was measured as net trajectory (change in vertical position divided by change in horizontal position between the beginning and end points of each path). In contrast, the number of larvae attaching to the bottom (herein defined as *settlers*), and both horizontal velocity and angular velocity (measured as rate of change in direction, RCDI) could be accurately quantified for movements by larvae in flows at all three speed settings. Our analyses of horizontal speed and RCDI were limited to those paths in which larvae did not contact the bottom.

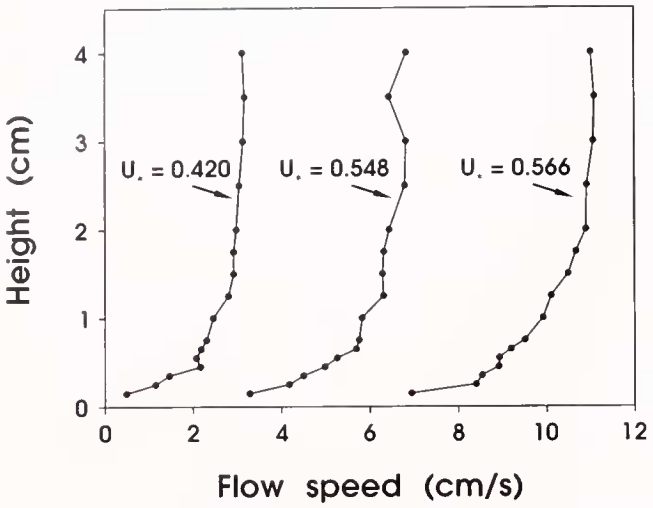

Figure 2. Velocity profiles for flowing water at each of the three flume settings used in experiments. From left to right, each profile is for flow with a free-stream speed of 2.8, 6.2, or 10.4 cm/s; shear velocity (U_*) for each flow is shown.

Results

Hydrodynamics

Velocity profiles, as well as shear velocity (U_*), for flow at each speed setting are shown in Figure 2. The average velocity ($\bar{U}$) for the slowest flow was 2.75 cm/s, for the intermediate flow was 6.21 cm/s, and for the fastest flow was 10.35 cm/s. Regressions used to calculate shear velocities accounted for more than 95% of the variation in the data in each case.

Settlement and behavior of larvae in flow

The behavior of oyster larvae in response to seawater (control) was markedly different from that in response to OCW and GGR (Kruskal-Wallis $\chi^2 = 12.74$, df = 2, $P = 0.002$). In seawater, the average trajectory was upward (2.9% slope), indicating that the larvae remain suspended above the flume bottom (Table I). An opposite effect was found in response to OCW and GGR—the average trajectory was downward (3.4% and 3.8% slope, Table I). Mean speeds at which downward-directed larvae moved in response to OCW and GGR were 1.7 mm/s (±0.6 mm/s SEM) and 1.8 mm/s (±0.7 mm/s SEM), respectively. After traveling downward in the water column, larvae approached the flume bottom and settled. Hence, the numbers of settlers in OCW at 2.8 cm/s flow speed and in GGR at 2.8 and 6.2 cm/s were significantly higher than those in seawater (control) at the same flow speeds (Table II, Kruskal-Wallis test). Although not statistically significant, there was a trend in the same direction for GGR at the fastest flow speed (10.4 cm/s, Table II).

Table I

Mean (±SEM) trajectory calculated as percent slope for each larval path in response to test or control solution at 2.8 cm/s flow speed

Solution	*n*	% Slope	Significance
SWC	39	2.93 ± 1.51	A
GGR	43	−3.80 ± 1.81	B
OCW	32	−3.42 ± 1.37	B

SWC = seawater control, GGR = 10^{-8} *M* glycyl-glycyl-L-arginine, OCW = adult-oyster-conditioned seawater. Trajectories were calculated as the ratio of change in vertical position to change in horizontal position between beginning and end points of paths. Positive values represent net upward motion and negative values represent net downward motion. Groups with different letters indicate a statistical difference at the $\alpha = 0.05/3 = 0.017$ level.

The exact height at which each larva swam within 4 mm of the flume bottom could not be precisely identified. Because the speed of fluid motion decreased close to the bottom (Fig. 2), determinations of velocity and rate of change in direction (RCDI) for horizontal movements by larvae reflected components of both active swimming and passive flow. We therefore made comparisons between test and control treatments separately at each speed setting. In this context, slower larval velocity indicates that a larva either swims closer to the flume bottom or indeed swims more slowly. In either case, a significant difference between stimulus and control treatments demonstrates a significant change in larval behavior. With these caveats in mind, we found that paths traveled by larvae in seawater (control) were significantly straighter (lower mean RCDI) and faster than those in OCW and GGR (Table III, Kruskal-Wallis $P < 0.05$ experimental-wise error, all comparisons). Remarkably, larvae often turned and swam upstream in response to GGR at 2.8 and 6.2 cm/s and to OCW at 2.8 cm/s (the only flow speed at which this solution was tested), but never in response to seawater (Fig. 3).

Table II

Mean (±SEM) number of larvae settling on the flume bottom in response to either test or control solution

	Flow speed (cm/s)		
Solution	2.8	6.2	10.4
SWC	1.00 ± 0.37 A	0.83 ± 0.31 A	1.67 ± 0.67 A
GGR	6.00 ± 1.84 B	6.00 ± 0.82 B	3.67 ± 0.88 A
OCW	4.50 ± 0.85 B	Not determined	Not determined

SWC = seawater control, GGR = 10^{-8} *M* glycyl-glycyl-L-arginine, OCW = adult-oyster-conditioned seawater. Groups with different letters indicate a statistical difference at the $\alpha = 0.05/3 = 0.017$ level using the Kruskal-Wallis chi square test.

Table III

Mean (±SEM) speed and rate of change in direction (RCDI) for horizontal movements by larvae, and number of larvae turning upstream in response to either test or control solution

		Movement by larvae		Number of larvae	
Flow speed (cm/s)	Solution	Speed (mm/s)	RCDI (degrees/s)	Observed	Moving upstream
2.8	SWC	1.69 ± 0.18 A	25.2 ± 4.0 A	2.5 ± 0.5	0
	GGR	0.49 ± 0.14 B	122.4 ± 20.6 B	3.2 ± 0.5	1.7 ± 0.6
	OCW	0.97 ± 0.21 B	93.7 ± 20.8 B	3.2 ± 0.5	1.2 ± 0.3
6.2	SWC	3.91 ± 0.41 A	22.4 ± 4.1 A	2.8 ± 0.4	0
	GGR	1.88 ± 0.38 B	81.0 ± 15.1 B	3.7 ± 0.5	0.4 ± 0.2
10.4	SWC	9.31 ± 0.55 A	32.9 ± 6.5 A	2.3 ± 0.3	0
	GGR	6.64 ± 0.60 B	155.6 ± 57.4 B	3.7 ± 0.3	0

SWC = seawater control, GGR = 10^{-8} *M* glycyl-glycyl-L-arginine, OCW = adult-oyster-conditioned seawater. Speed and RCDI were limited to those paths in which larvae did not contact the bottom, whereas all paths in the field of view were examined for movement upstream. Groups with different letters indicate a statistical difference at the $\alpha = 0.05/3 = 0.017$ level using the Kruskal-Wallis chi square test.

Discussion

These results show that waterborne chemical cues evoke settlement in flow by planktonic oyster larvae. Pediveligers responded to dissolved compounds by moving downward in the water column, then swimming in slow curved paths and attaching to the flume bottom. The behavior we observed in flume flows was essentially identical to that previously described in still water (Tamburri *et al.*, 1992; Zimmer-Faust *et al.*, in press). Whereas still-water assays are valuable in describing behavioral responses, both flume and field experiments are required to identify those hydrodynamic environments in which such behavior allows larvae to select settlement sites.

Important insights to settlement processes can be gained by considering the relationship between hydrodynamics and larvae swimming and tumbling in bottom boundary-layer flows (Jonsson *et al.*, 1991; Mullineaux and Butman, 1991; Pawlik *et al.*, 1991; Grassle *et al.*, 1992; Pawlik and Butman, 1993). When flow speeds and shear velocities were below critical thresholds at which larvae become transported as bed load (about 4–5 cm/s and 0.25 cm/s, respectively), in the absence of waterborne chemical cues, weakly swimming cockle (*Cerastoderma edule*, Jonnson *et al.*, 1991), worm (*Phragmatopoma lapidosa californica*, Pawlik and Butman, 1993), and oyster larvae (this study) all propelled themselves upward to remain suspended in the water column. This behavioral response allows the larvae to avoid settling in relatively slow flows even though physical attachment is possible (Pawlik and Butman, 1993). At faster flow speeds and higher shear velocities, where bed-load transport occurs but resuspension is rare, both cockle and worm larvae become trapped in the near-bed flow and roll along the bottom (Jonnson *et al.*, 1991; Pawlik and Butman, 1993). Perhaps we did not observe rolling for oyster pediveligers because they were introduced at 4 cm above the bottom. At flow speeds of 6.2 and 10.4 cm/s, oyster larvae would have had only about 10–20 s after introduction to either sink or swim downward before being swept over the working section of the flume. Indeed, visual observations of oyster larvae moving downstream in a larger flume (4.8-m long) previously indicated that larvae were always close (<2 mm) to the bed (Turner *et al.*, 1994). If the hydrodynamic regime confines larvae close to the bed (Jonsson *et al.*, 1991), larvae will not need to settle very far to contact the bottom. Even a small change in vertical movement caused by a waterborne chemical cue might thus be important in mediating settlement under some flow conditions.

The Rouse number reflects the strength of the downward transport of larvae due to gravitational sinking and swimming, relative to the upward transport of larvae due to turbulent mixing (Gross *et al.*, 1992; Eckman *et al.*, 1994). This number is a dimensionless ratio (w_j/kU_*), where w_j is downward transport due to larval sinking and swimming, k is von Karman's constant (=0.41), and U_* is shear velocity. At Rouse numbers greater than 0.75, larval swimming and sinking can have a substantial impact on settlement from a turbulent, bottom boundary layer (Gross *et al.*, 1992). In response to a waterborne chemical cue, oyster pediveligers move downward at average and maximum speeds of 1.8 mm/s and 3.1 mm/s, respectively (Turner *et al.*, 1994; this study). Furthermore, shear velocity of water flowing over an oyster reef scales at 0.17-times the free-stream speed (Wright *et al.*, 1990). We observed a Rouse number greater than 0.75 for flow speeds below 3.5 cm/s, indicating that settlement is not inhibited by turbulence. At flow speeds of 6 cm/s, only the most rapidly swimming larvae (vertical

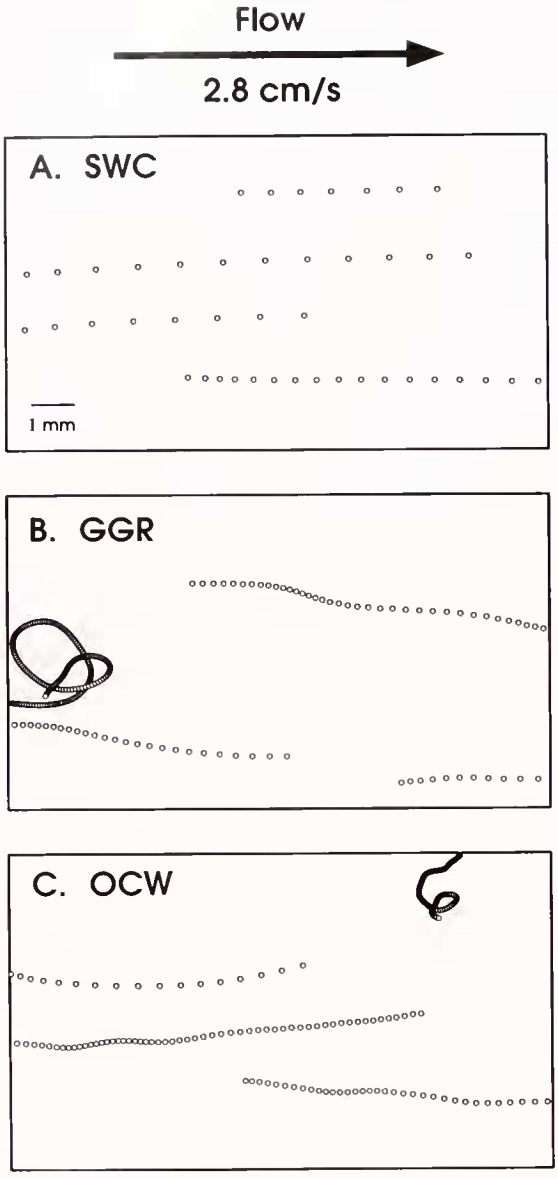

Figure 3. Computer-digitized video records showing the horizontal paths of larvae moving within 4 mm of the flume bottom and entering the 1.2- × 0.7-cm field viewed by the overhead camera. The paths generated for four larvae appear in each box. Each path of dots presents the position of a larva at consecutive, one-frame intervals with video collected at 30 frames/s. We selected the paths to illustrate the various movement patterns (including upstream swimming) observed in flowing water at 2.8 cm/s. These data are for larvae exposed to either (A) seawater control (SWC), (B) 10^{-8} *M* glycyl-glycyl-L-arginine (GGR), or (C) oyster-conditioned seawater (OCW). Paths are straighter and faster in response to SWC than to either GGR or OCW.

velocities > 3 mm/s) can overcome turbulent transport. Remarkably, these speeds are common in water flowing above oyster reefs in tidal estuaries (Breitburg *et al.*, 1995).

A model for benthic-habitat site selection by weakly swimming invertebrate larvae has been proposed by Butman and Grassle (1992). In this model, larvae are hypothesized to move up and down in the water column close to the bottom, while being transported by flow, and to test substrates on contact. Selection is thus accomplished by active acceptance or rejection of touchdown sites. We suggest, at least for oyster pediveligers, that behavioral response to a waterborne chemical cue is an additional factor in habitat selection. Oyster larvae rapidly respond (within 5 s of initial exposure) to dissolved substances produced by juvenile and adult conspecifics and by bacteria in biofilms on the surface of oyster shell (Tamburri *et al.*, 1992; Zimmer-Faust *et al.*, in press). These stimulatory compounds are low molecular weight peptides with arginine at the C-terminal; at concentrations of 10^{-10} *M*, or lower, they effectively cause downward-directed movements by oyster larvae in the water column (Zimmer-Faust and Tamburri, 1994). Because this behavioral response does not require a chemical gradient, induction of settlement should be possible even in turbulent-flow environments. Presumably, downward movements increase the probability that oyster larvae will be swept into contact with preferred benthic substrata by near-bed turbulent eddies.

Juvenile and adult oysters commonly form extensive aggregations (10,000 m^2, and beyond) at high densities (15,000 individuals/m^2) in benthic estuarine habitats (Bahr, 1981). Waterborne compounds produced by post-metamorphic oysters will thus be distributed over large areas, rather than confined to isolated point sources. Field data further indicate that flow velocities measured 2–10 cm above oyster reefs rarely exceed 7 cm/s (Breitburg *et al.*, 1995). This means that oyster larvae drifting near the bottom will likely pass over cued substratum for several minutes, long enough for the induction of a settlement response.

We suggest that the effectiveness of waterborne settlement cues may be greatest in environments similar to those in which oyster larvae settle. Perhaps the capacity of dissolved compounds to influence settlement is linked to cue production and, therefore, is most important in habitats that have large aggregations of post-metamorphic conspecifics or food resources. Waterborne cues might also function as general chemical signatures indicating the presence of preferred substrates, such as those provided within coral reefs, kelp forests, and organic-rich mud flats. Although the effects of waterborne chemical cues may be profound, the extent to which such cues influence settlement remains largely unexplored.

Acknowledgments

This research was sponsored by awards from the National Science Foundation (OCE 94-16749), South Car-

olina Sea Grant Consortium (P-M-2F, P-M-2K, R-92-88), Office of Naval Research (N0014-K-82-646), Slocum-Lunz Foundation, Lerner-Gray Fund for Marine Research, and Sigma Xi. We thank K. Kurkowski and V. L. Shaffer for generously providing larvae, C. C. Gee for assistance in illustrating larval paths, and N. D. Pentcheff and Drs. A. W. Decho, M. W. Luckenbach, and S. E. Stancyk for their comments, which greatly improved earlier drafts of this manuscript.

Literature Cited

Bahr, L. M. 1981. The ecology of intertidal oyster reefs of the South Atlantic coast: a community profile. *U.S. Fish Wildl. Serv.* FWS/OBS-81/15.

Bonar, D. B., S. L. Coon, M. Walch, R. M. Weiner, and W. Fitt. 1990. Control of oyster settlement and metamorphosis by endogenous and exogenous chemical cues. *Bull. Mar. Sci.* **46:** 484–498.

Breitburg, D. L., M. A. Palmer, and T. Loher. 1995. Larval distributions and the spatial patterns of settlement of an oyster reef fish: responses to flow and structure. *Mar. Ecol. Prog. Ser.* **125:** 45–60.

Burke, R. D. 1983. The induction of metamorphosis of marine invertebrate larvae: stimulus and response. *Can. J. Zool.* **61:** 1701–1719.

Burke, R. D. 1984. Pheromonal control of metamorphosis in the Pacific sand dollar, *Dendraster excentricus*. *Science* **225:** 442–443.

Butman, C. A. 1986. Larval settlement of soft-sediment invertebrates: some predictions based on an analysis of near-bottom velocity profiles. Pp. 487–513 in *Marine Interfaces Ecohydrodynamics*, J. C. J. Nihoul, ed. Elsevier, Amsterdam.

Butman, C. A. 1987. Larval settlement of soft-sediment invertebrates: the spatial scales of pattern explained by habitat selection and the emerging role of hydrodynamic processes. *Oceanogr. Mar. Biol. Annu. Rev.* **25:** 113–165.

Butman, C. A. 1989. Sediment-trap experiments on the importance of hydrodynamical processes in distributing settling invertebrate larvae in near-bottom waters. *J. Exp. Mar. Biol. Ecol.* **134:** 37–88.

Butman, C. A., and J. P. Grassle. 1992. Active habitat selection by *Capitella* sp. larvae: I. two-choice experiments in still water and flume flow. *J. Mar. Res.* **50:** 669–715.

Crisp, D. J. 1984. Overview of research on marine invertebrate larvae, 1940–1980. Pp. 103–126 in *Marine Biodeterioration: An Interdisciplinary Study*, J. D. Costlow and R. C. Tipper, eds. Naval Institute, Annapolis, Maryland.

Crisp, D. J., and P. S. Meadows. 1962. The chemical basis of gregariousness in cirripedes. *Proc. Roy. Soc. Lond. B* **156:** 500–520.

Eckman, J. E. 1990. A model of passive settlement by planktonic larvae onto bottoms of differing roughness. *Limnol. Oceanogr.* **35:** 887–901.

Eckman, J. E., F. E. Werner, and T. F. Gross. 1994. Modeling some effects of behavior on larval settlement in a turbulent boundary layer. *Deep-Sea Res.* **41:** 185–208.

Gaines, S. D., S. Brown, and J. Roughgarden. 1985. Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia* **67:** 267–272.

Grassle, J. P., C. A. Butman, and S. W. Mills. 1992. Active habitat selection by *Capitella* sp. I larvae: II. multiple choice experiments in still water and flume flows. *J. Mar. Res.* **50:** 717–743.

Grosberg, R. K. 1987. Limited dispersal and proximity-dependent mating success in the colonial ascidian *Botryllus schlosseri*. *Evolution* **41:** 372–384.

Gross, T. F., F. E. Werner, and J. E. Eckman. 1992. Numerical modeling of larval settlement in turbulent bottom boundary layers. *J. Mar. Res.* **50:** 611–642.

Johnson, L. E., and R. R. Strathmann. 1989. Settling barnacles avoid substrata previously occupied by a mobile predator. *J. Exp. Mar. Biol. Ecol.* **128:** 87–103.

Jonsson, P. R., C. André, and M. Lindegrath. 1991. Swimming behavior of marine bivalve larvae in a flume boundary layer flow: evidence for near-bottom confinement. *Mar. Ecol. Prog. Ser.* **79:** 67–76.

Levitan, D. R. 1991. Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. *Biol. Bull.* **181:** 261–268.

Menge, B. A. 1991. Relative importance of recruitment and other causes of variation in rocky intertidal community structure. *J. Exp. Mar. Biol. Ecol.* **146:** 69–100.

Morse, A. N. C., and D. E. Morse. 1991. Enzymatic characterization of the morphogen recognized by *Agaricia humilis* (Scleractinian coral) larvae. *Biol. Bull.* **181:** 104–122.

Morse, D. E. 1990. Recent progress in larval settlement: closing the gap between molecular biology and ecology. *Bull. Mar. Sci.* **46:** 465–483.

Morse, D. E., N. Hooker, H. Duncan, and L. Jensen. 1979. γ-Aminobutyric acid, a neurotransmitter, induces planktonic abalone larvae to settle and begin metamorphosis. *Science* **204:** 407–410.

Mullineaux, L. S., and C. A. Butman. 1991. Initial contact, exploration and attachment of barnacle cyprids settling in flow. *Mar. Biol.* **110:** 93–103.

Nowell, A. R. M., P. A. Jumars, and J. E. Eckman. 1981. Effects of biological activity on the entrainment of marine sediments. *Mar. Geol.* **42:** 133–153.

Pawlik, J. R. 1992. Chemical ecology of the settlement of benthic marine invertebrates. *Oceanogr. Mar. Biol. Annu. Rev.* **30:** 273–335.

Pawlik, J. R., and C. A. Butman. 1993. Settlement of a marine tube worm as a function of current velocity: interacting effects of hydrodynamics and behavior. *Limnol. Oceanogr.* **38:** 1730–1740.

Pawlik, J. R., C. A. Butman, and V. R. Starczak. 1991. Hydrodynamic facilitation of gregarious settlement of a reef-building tube worm. *Science* **251:** 421–424.

Roughgarden, J., S. D. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life-cycles. *Science* **241:** 1460–1466.

Tamburri, M. N., and R. K. Zimmer-Faust. 1996. Suspension-feeding: basic mechanisms controlling recognition and ingestion of larvae. *Limnol. Oceanogr.* **41:** 1188–1197.

Tamburri, M. N., R. K. Zimmer-Faust, and M. L. Tamplin. 1992. Natural sources and properties of chemical inducers mediating settlement of oyster larvae: a re-examination. *Biol. Bull.* **183:** 327–338.

Turner, E. J., R. K. Zimmer-Faust, M. A. Palmer, M. Luckenbach, and N. D. Pentcheff. 1994. Settlement of oyster (*Crassostrea virginica*) larvae: effects of water flow and a water-soluble chemical cue. *Limnol. Oceanogr.* **39:** 1579–1593.

Underwood, A. J., and P. G. Fairweather. 1989. Supply-side ecology and benthic marine assemblages. *Trends Ecol. Evol.* **4:** 16–20.

Woodin, S. A. 1987. Recruitment of infauna—positive or negative cues? *Am. Zool.* **31:** 797–807.

Wright, L. D., R. A. Gammisch, and R. J. Byrne. 1990. Hydraulic roughness and mobility of three oyster-bed artificial substrate materials. *J. Coastal Res.* **6:** 867–878.

Zimmer-Faust, R. K., and M. N. Tamburri. 1994. Chemical identity and ecological implications of a waterborne, larval settlement cue. *Limnol. Oceanogr.* **39:** 1075–1087.

Zimmer-Faust, R. K., M. N. Tamburri, and A. W. Decho. In press. Chemosensory ecology of oyster larvae: benthic-pelagic coupling. *Mar. Freshwat. Behav. Physiol.*